ANNUAL FLUCTUATIONS IN THE ABUNDANCE OF MARINE ZOÖPLANKTON [1]

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From the time of the earliest oceanographic expeditions, it has been recognized that the open oceans are more densely populated in high northern and southern latitudes than in the tropical belts, and that the richest areas of all are boreal coastal waters. But even in these fertile zones, the abundance and character of the plankton is known to fluctuate from time to time. Perhaps the most obvious change is a seasonal one. During the spring a wave of reproduction commonly follows the winter period of scarcity, and later in the summer there may or may not be a second period of increase. However, the seasonal cycle is not constant from year to year either in the numbers or in the species of animals produced. In certain cases, annual changes of this sort have been thought due to fluctuations in the amount of " foreign " water entering a given area from neighboring regions. As a consequence, plankton studies in recent years have frequently centered on a search for " indicator " species which would reveal the presence of intruded water and give a clue to its origin. Possibilities were foreseen of the practical use of such " indicators " in forecasting the success of the fisheries or even in solving complex hydrographic problems (for a recent bibliography, see Russell, 1939; additional references, Pierce and Orton, 1939; Redfield, 1939; Sømme, 1934; Bigelow and Sears, 1937; Report Newfoundland Fisheries Research Commission, 1932; Frost, Lindsay, and Thompson, 1933; Thompson and Frost, 1935, 1936).

By far the most extensive plankton investigations based on the study of " indicators " of this sort has been undertaken at Plymouth, England (Russell, 1939). Of the results obtained perhaps the most suggestive are derived from the fluctuations in abundance of the two chaetognaths, *Sagitta setosa* and *Sagitta elegans,* since the former has almost entirely replaced the latter in the years following 1931. At the same time, in the Plymouth region, there has been a continued impoverishment of the phosphates in the water, a scarcity of fish larvae, and finally a failure of the herring fishery. Since it has been concluded that " *S. setosa* pre-

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dominates off Plymouth when the easterly element in the Dover Straits current is suppressed and the flow of Atlantic water into the North Sea from the north is strong (Carruthers theory) " (Russell, 1935, p. 328), the unusual conditions in the plankton are believed due primarily to changes in water circulation.

There are, however, examples of fluctuations among the planktonic animals of the Plymouth region which are not so clearly correlated with a mixing of water masses. Thus, the two species of the siphonophore genus *Muggiaea*—inhabitants of warm coastal waters generally—do not appear together in the waters off Plymouth: *M. atlantica* has been taken regularly at the Seven Stones lightship between 1913 and 1925, whereas *M. kochii* replaced it after 1925—at least until 1934 (Russell, 1934). It is suspected that both these species are " indicators " of coastal waters from the south, i.e., the shallower waters bordering on the Bay of Biscay. If this is true, there must be some factor (or factors) other than transport by currents responsible for fluctuations of species such as these which are presumably inhabitants of the same water mass. Such differences would be extremely difficult to distinguish in an area such as Plymouth, which is beset by strong tidal currents as well as by ocean currents.

It is the purpose of this paper to call attention to the occurrence of marked fluctuations in the zoöplankton on the continental shelf south of Cape Cod, a region which is not subject to such irregular mass incursions of " foreign " water as invade the Plymouth area. Such fluctuations as those just cited for the two species of *Muggiaea* may be due in part, at least, to limiting factors as subtle as those controlling the size of the different year classes among fish.

In the coastal waters from Cape Cod to Chesapeake Bay, plankton samples were collected by the U. S. Bureau of Fisheries on 23 cruises during the first half of the years 1929–1932 (Bigelow and Sears, 1939). These observations have been supplemented by stations on a section crossing the shelf off Montauk Point on ten occasions between October, 1937 and June, 1939 (Clarke, 1940) and by collections made at the whistle buoy 3 miles off Martha's Vineyard in 1935–1936 (Sta. 3, Clarke and Zinn, 1937) and on other occasions during the summers of 1937, 1938, and 1939 (unpublished data). These data clearly show important fluctuations not only in the total mass of zoöplankton, but also in the abundance of some of the more common species. Here, the waters undergo essentially the same seasonal changes in temperature and salinity each year (Bigelow, 1933; Bigelow and Sears, 1935; Clarke, 1940) following the cycle which is characteristic of boreal waters generally. A considerable amount of highly saline water from beyond the edge of the continental shelf must enter this region each year to compensate for the large inflow of river water and rain (Iselin, 1939). However, any transport of plankton into this coastal area by this "slope" water (Iselin, 1936, p. 11, Fig. 2) is slight, since there is always a sharp boundary between the populations of the coastal waters and those offshore. In fact, on the routine cruises now being run SSE from Montauk Point to a point the other side of the Gulf Stream, it is usually possible to sort the catches by casual inspection, according to the locality of capture. The catches on the continental shelf consist essentially of the common coastal species (see Bigelow and Sears, 1939); while those in the "slope" water are composed of *Metridia lucens,* rather than *Calanus* or *Centropages,* as the outstanding copepod, *Sagitta enflata,* as the characteristic chaetognath, and usually salps (*Salpa fusiformis, Iasis zonaria*) in some quantity as well as other typically oceanic species (unpublished data; Clarke, 1940). While *Metridia,* it is true, occurs in some numbers over the outer half of the shelf, particularly in the north, we seldom find other oceanic species more than 10–15 miles inside the 200-meter contour.[2] Hence, while there is some possibility of "contamination" by offshore animals in the region under consideration, it seldom affects any considerable area and never for any length of time.

In addition to the increments derived from the "slope" water, our coastal area also receives water in small quantities from the vicinity of Nantucket Shoals, particularly during the spring. We have little reason to suppose, however, that this has any marked effect on the zoöplankton, for during the spring of 1932, when several intrusions of colder water from the north were observed (Bigelow, 1933), the only noticeable effect of this water movement was the introduction of a meager number of *Calanus hyperboreus* and *Oikopleura labradoriensis* into the area south of Cape Cod (Bigelow and Sears, 1939, p. 247). Actually, during the spring, when flooding from the north most often occurs, the chief effect would be a dilution, since at this season the population in the waters of the Gulf of Maine is at its minimum (Bigelow, 1926). Were there to be an intrusion from this source later in the summer, it is unlikely that the nature of the plankton would be appreciably affected, since catches made in September (1939) on the western part of George's Bank and over the continental shelf between Montauk Point and Martha's Vineyard (unpublished data) were of much the same richness and type, chiefly *Centropages typicus.*

[2] The waters may become "overridden" temporarily with warm-water species which reproduce rapidly (i.e., *Salpa fusiformis*—July 6 to mid-August, 1929). But the enormous quantities of these (3,000–5,000 cc. per 20-minute tow with a meter net) are due to local propagation and are not an indication of an unusually large mixing of "slope" water, because other oceanic species occur only as traces.

Nevertheless in this region between Cape Cod and Chesapeake Bay—an area biologically isolated from the "slope" water offshore and only slightly contaminated by the plankton of Nantucket Shoals—*Calanus finmarchicus* showed a 10-fold fluctuation in abundance (by volume) at the season of its greatest richness during the years 1929–1932 (Fig. 1). In addition, when the richest of these periods (July, 1931) is com-

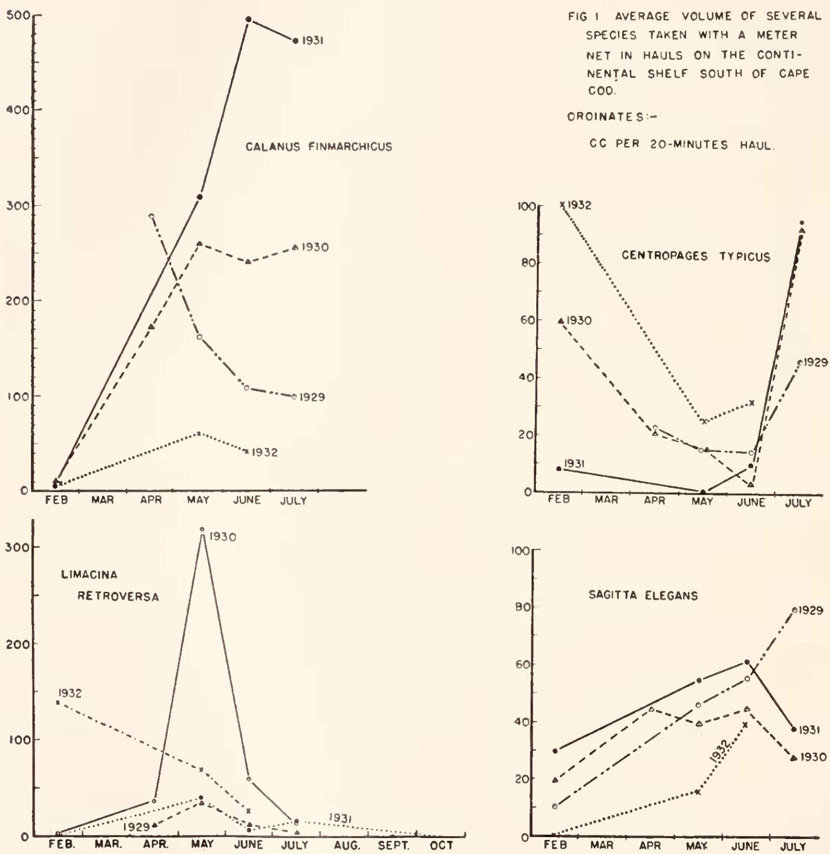

FIG I AVERAGE VOLUME OF SEVERAL SPECIES TAKEN WITH A METER NET IN HAULS ON THE CONTINENTAL SHELF SOUTH OF CAPE COD.
ORDINATES:— CC PER 20-MINUTES HAUL.

pared with the very poor periods of a few years later (July 1937–1939), a 600-fold difference (by volume) is revealed. Equally great fluctuations in the stock of *Calanus* have been encountered south of Woods Hole in other years when no extensive surveys were undertaken. This copepod was virtually unobtainable in the vicinity of Woods Hole during the past three summers, although it was abundant during 1935 and 1936 (Clarke and Zinn, 1937).

TABLE I

Species	Year of greatest abundance by volume	Year of least abundance by volume
Calanus finmarchicus	1931	1932
Limacina retroversa	1930	1931
Sagitta elegans	1929, 1931	1932
Centropages typicus	1932	1931
Aglantha digitale	1932	1931
Euthemisto compressa	1930	?

Other individual species studied quantitatively during 1929–1932 have similarly undergone marked fluctuations (more especially over the northern half of the area), notably *Limacina retroversa* (12-fold, Fig.

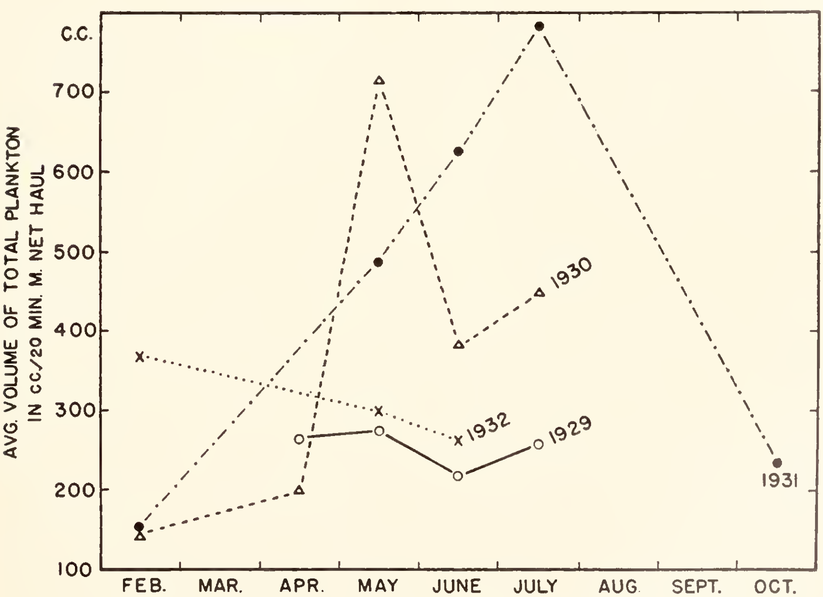

FIG. 2. Average volumes of total plankton.

1), and to a lesser degree *Sagitta elegans* and *Centropages typicus* (Fig. 1). Other members of the plankton which ordinarily occur as odd specimens may become sufficiently numerous in certain years to form a measurable proportion of the total. Such was the case for *Euthemisto compressa* in 1930 and *Aglantha digitale* in 1932. Furthermore, it appears that these fluctuations occur independently of one another—a year (1931) rich in *Calanus* being poor in *Limacina* or a year (1932) rich in *Centropages* being poor in *Calanus,* etc. (See Table I.)

Not only do individual species exhibit these marked fluctuations, but in addition the plankton as a whole varies in abundance from year to

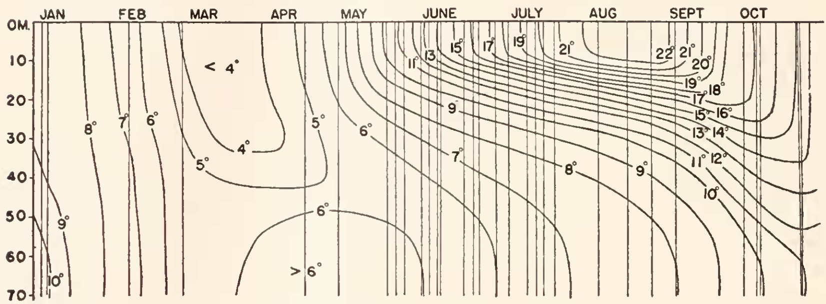

FIG. 3. Average temperatures throughout the year on the continental shelf off Montauk Point, based on all available data.

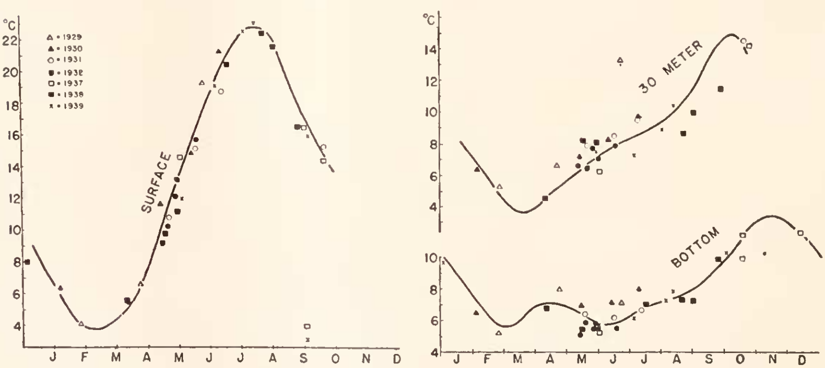

FIG. 4. Departures of temperature from the average seasonal cycle at the surface, 30 meters, and the bottom, for 1929–1932 and 1937–1939, at stations half-way across the continental shelf off Montauk Point.

year (Fig. 2). In the relatively short series of observations (1929–1932), plankton was much more plentiful during the warm winter of 1932 than in the other winters, especially in the south (Bigelow and Sears, 1939), and this condition seemingly continued through late April (judging from a few vertical hauls of about 400 cc. per 20-minute tow—unpublished data). By May and June of that same year, however, the plankton was distinctly sparse—in fact, as sparse as in 1929. On the other hand, although the plankton had been very poor in the winter of 1931, it was decidedly richer than average during every other month of that year when surveys were made. Earlier surveys had likewise shown similar fluctuations, the plankton being unusually abundant during the cold summer of 1916 and scarce during the warm summer of 1913 (Bigelow, 1926).

Without a longer series of observations we can offer little explanation for these fluctuations. It has been suggested that temperature is the factor in our area which prevents *Calanus* from entering the upper water layers (15–22° C.) in the summer months and restricts this species to the deeper water (7–12° C., Fig. 3). Nevertheless, it does not appear likely that temperature *per se* causes these annual changes in abundance of *Calanus* since the temperature differences are only 1–2° C. between "warm" and "cold" years (Fig. 4)—a difference which would hardly limit the distribution of an animal living over such a wide temperature range as *Calanus*.

We have also made a cursory examination of the salinities and found them to be somewhat more variable locally than the temperatures, from year to year, and even from month to month, especially in the surface layers. However, there appears to be no abnormal mixture of offshore water, the variability seemingly being caused by irregularities in the local rainfall and the inflow from the rivers.

Since the occurrence of wide fluctuations in the abundance of zooplankton in our coastal area now seems well established, further investigation of the consequences of such variation is called for. It is to be hoped, for instance, that a correlation may be found between the richness of the plankton and the fluctuations in the abundance of a commercially important fish such as the mackerel (Sette, 1940), which feeds upon the plankton.

Summary

The abundance of the zoöplankton in the waters overlying the continental shelf between Cape Cod and Chesapeake Bay is shown to be subject to severe annual fluctuations in respect both to individual species and to the total population. Yearly variations of this sort in British waters have been attributed to mass incursions of water from outside sources; but since no great annual differences in the exchange of water masses have been found in the coastal regions treated in this study, our data strongly indicate that important fluctuations in the plankton may occur in relatively undisturbed areas. These changes in the plankton

are not found to be correlated directly with gross environmental changes and therefore must be due to an indirect action of physical or biological factors.

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